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BATHYMETRIC PATTERNS OF BODY SIZE IN DEEP-SEA GASTROPODS

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Abstract.—The shift to smaller body size in marine invertebrates at the deep-sea threshold and size-depth clines within the deep-sea ecosystem are global biogeographic phenomena that remain poorly understood. We present the first standardized measurements of larval and adult size among ecologically and phylogenetically similar species across a broad and continuous depth range, using the largest family of deep-sea gastropods (the Turridae). Size at all life stages increases significantly with depth from the upper bathyal region to the abyssal plain. These consistent clines may result from selection favoring larger size at greater depths because of its metabolic and competitive advantages. The unusually small size of deep-sea mollusks, in general, may represent an independent evolutionary process that favors invasion by inshore taxa composed of small organisms.

Key words.—Bathymetric clines, benthic, body size, deep sea, gastropods.

The most conspicuous feature of the deep-sea invertebrate fauna is the small size of most species compared to their shallow-water counterparts (Gage and Tyler 1991). Surprisingly little research has been devoted to understanding this very fundamental difference between coastal marine and deep-sea ecosystems. The earliest critical attempt was Thiel's (1975, 1979) size-structure hypothesis. Synthesizing existing data, Thiel showed that the density of the macrofauna decreased more rapidly with depth than did the density of the more abundant and smaller meiofauna. This implied a decrease in average organism size with depth. The size-structure hypothesis attributed this to a balance of scaling factors related to food availability. The decrease in nutrient input with depth would seem to favor larger size because larger organisms, including deep-sea species (Mahaut et al. 1995), are more metabolically efficient per unit mass (Peters 1983). Because size appeared to decrease with depth, the size-structure hypothesis held that the advantages of metabolic efficiency must be counteracted by other factors. It was theorized that food constraints either become too severe to sustain large animals because of their large total energetic demand on the environment or do not permit reproductively viable population sizes to develop for large organisms. Although the theory was directed at explaining geographic patterns of average body size resulting from shifts in the representation of major functional groups, the meio- and macrofauna, the underlying mechanisms invoked population density and the

adaptive consequences of body size in individual species. Optimality models of size in marine invertebrates (Sebens 1987) also predict a general decrease in size as the rate of energy intake is depressed and foraging costs increase with increased depth (Rex and Etter 1998).

Subsequent tests of the size-structure hypothesis have produced conflicting results. The primary evidence on which the theory was based, a nonlinear relationship between meio- and macrofaunal abundances, has not been consistently supported by later sampling studies (Shirayama 1983; Sibuet et al. 1989). Body size in a wide variety of deep-sea taxa and functional groups has been reported to increase, decrease, or show no consistent pattern with depth (reviewed in Gage and Tyler 1991; Rex and Etter 1998). Most studies suffer from two methodological problems that hinder interpreting size as an adaptive response to the deep-sea environment. First, size typically has been measured as average biomass or some average physical dimension in organisms from whole communities or higher taxa—often those representing a tremendous diversity of morphology, degree of calcification, and lifestyle. Inferring adaptation in a precise way requires analyses within species or among ecologically comparable species. Second, the use of whole dredged samples of populations to ascertain average body size is apt to merely reflect the recent history of recruitment and population dynamics, which can be seasonally and spatially variable in the deep sea (Gage and Tyler 1991). Size as an adaptation is more accurately
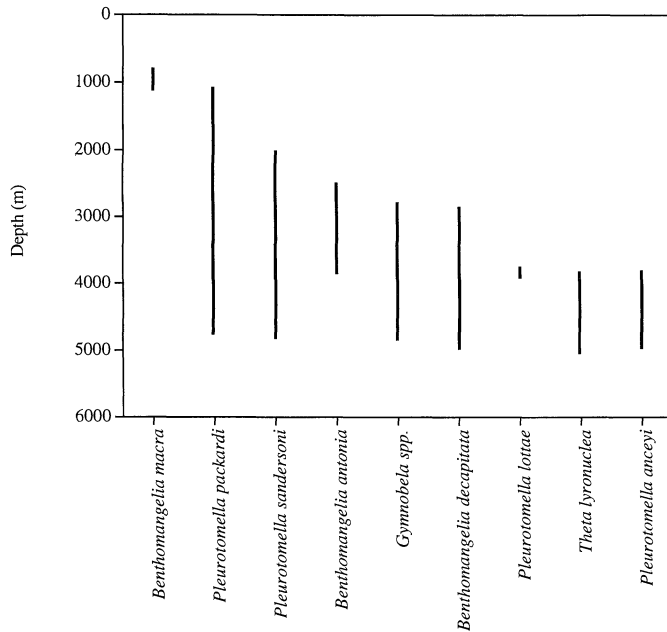
FIG. 1. The depth distributions of nine species of deep-sea turrid gastropods used in the analysis of bathymetric patterns of body size. All populations were collected by epibenthic sleds in the western North Atlantic south of New England. See Sanders et al. (1965), Hessler and Sanders (1967), and Rex (1976, 1981) for more on collecting methods. See Bouchet and Warén (1980) for systematic descriptions. *Gymnobela* spp. refers to a taxonomically unresolved assemblage that may represent more than one species.

revealed in final size attained or size standardized to a common growth stage. Only a few studies meet these criteria: analyses of maximum size in the upper bathyal brittle star *Ophiura sarsii* (Fujita 1992), size of instars in the lower bathyal and abyssal isopod *Eurycope iphthima* (Wilson 1983), and shell size at common growth stages in several snail species (Rex and Etter 1998). In contrast to theoretical predictions, these studies showed a strong statistically significant trend for size to increase with depth *within* individual species. Here, we present the first standardized measurements of larval and adult size among ecologically and phylogenetically similar species across a broad and continuous depth range.

MATERIALS AND METHODS

We analyzed shell size in nine species of the gastropod family Turridae distributed along a depth gradient from upper bathyal (808 m) to abyssal depths (5018 m) in the western North Atlantic (Fig. 1). The Turridae is the largest family of deep-sea gastropods (Bouchet and Warén 1980). It is a guild of predators specializing on polychaete worms (Shimek, 1983a,b,c). All species analyzed here have planktotrophic (swimming-feeding) larval development and share the same basic shell architecture (Bouchet and Warén 1980; Rex and Warén 1982; Killingley and Rex 1985; Stuart and Rex 1994). Eight of the nine turrids are phenotypically coherent species (Bouchet and Warén 1980). *Gymnobela* spp. is a taxonomically difficult group that may represent more than one species. We include it because our analysis is concerned primarily with geographic patterns of size among taxa within a family.

Gastropods are particularly useful for this kind of analysis because their life history is retained in shell form and their hard carbonate shells allow precise measurement of size that is unaffected by artifacts of collection and preservation, as often occurs in soft-bodied taxa. We examine size-depth trends at two common growth stages, the larval shell (protoconch) at the larval-adult transition and the end of the first adult whorl. Protoconch size was measured as the maximum width of the larval shell. Width is used because the apex of larval shells is sometimes corroded, thus making it impossible to accurately measure the height of the larval shell. Adult first whorl size is the height plus width at the end of the first postlarval whorl (Gould 1969). We also estimate final adult size attained. The latter is very subject to sampling error, especially in such sparsely distributed populations. Large specimens are rarest and may simply not have been caught by individual bottom trawls. We approach this problem in two ways, by selecting the largest individuals of each species at each sampling location and the largest individuals recovered in successive 500-m depth intervals. A detailed account of shell orientation and exact measurements taken is given in Rex and Etter (1990). Size variables were measured microscopically by using a computerized image analysis system and the software NIH-IMAGE.

RESULTS AND DISCUSSION

Figure 2 shows that standardized larval and adult sizes and estimates of maximum size attained all increase in a regular and highly significant way with increased depth among members of the Turridae. It is difficult to separate statistically the within- and among-species contributions to these patterns in a precise way. When ANOVAs are used to partition the individual variance in size among the effects of depth, species, and species-depth interactions, there remain significant independent depth effects ($F_{1,271} = 15.869$, $P < 0.0001$; $F_{1,209} = 18.540$, $P < 0.0001$; and $F_{1,9} = 6.208$, $P < 0.0343$ for larval size, adult size, and maximum size per 500 m, respectively), which we presume to represent an among-species component to the increase in size. Elsewhere, Rex and Etter (1998) showed that there is a strong tendency for larval and adult size to increase significantly with depth within species of deep-sea gastropods; although these species, unlike the Turridae analyzed here, represent a wide variety of life histories, trophic types, and phylogenetic affinities. There was no indication that size decreases with depth. For most of the turrid species in Figures 1 and 2, samples are too small to convincingly examine within-species patterns. However, there are five significant ($P < 0.02$ to $P < 0.0001$) cases of size-depth regressions for standardized variables (protoconch width or whorl 1 size) in four taxa, *Benthomangelia macra, Benthomangelia antonia, Gymnobela* spp., and *Pleurotomella lottae*. All of these significant regressions are positive. These inter- and intraspecific patterns do not support earlier predictions that size should decrease with depth.

The causes of increased size with depth are difficult to ascertain for such an inaccessible environment where our knowledge of these species is based exclusively on remote sampling. Temperature gradients, one of the most commonly invoked adaptive and nonadaptive causes of body size clines
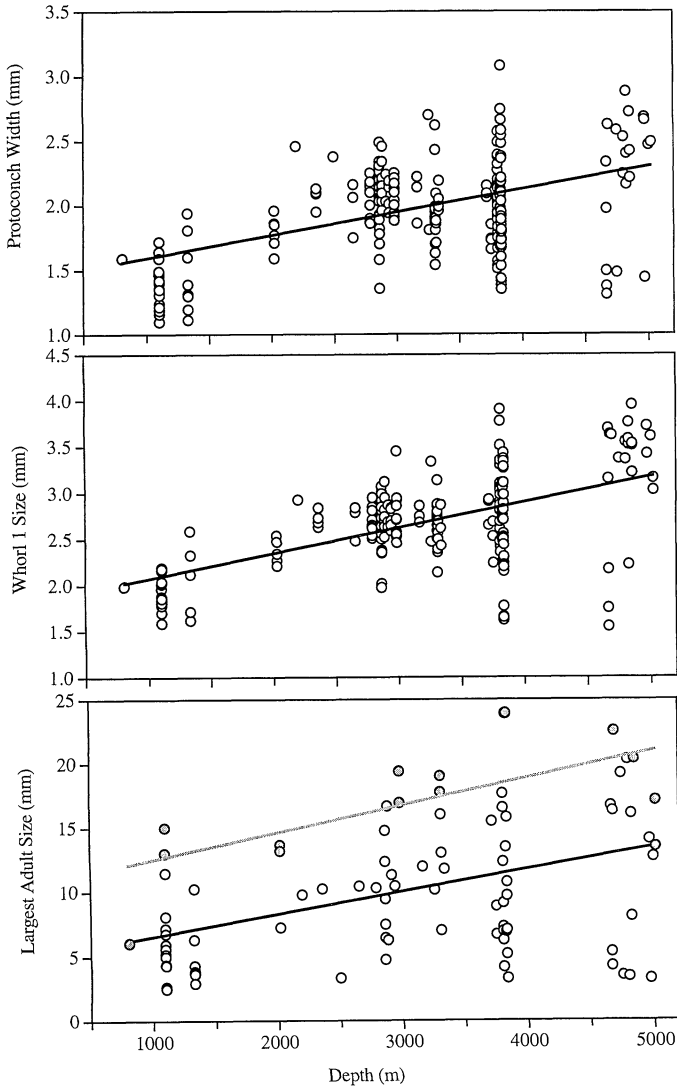
FIG. 2. Bathymetric patterns of larval size, size at the end of the first adult whorl, and largest adult size in species of turrid gastropods collected from the western North Atlantic. Largest size was estimated in two ways. Open circles are the largest individuals of each species at each sampling size. Closed circles are the largest two individuals encountered in each 500-m depth interval. Larval and adult sizes increase significantly with depth. Analyses were conducted using raw data. Regression equations and their statistics as follows: protoconch width: $y = 0.697 + 0.000101x$, $df = 288$, $r^2 = 0.274$, $F = 108.197$, $P < 0.0001$; whorl 1 size: $y = 1.798 + 0.000276x$, $df = 226$, $r^2 = 0.298$, $F = 95.692$, $P < 0.0001$; largest adults: $y = 4.833 + 0.002x$, $df = 83$, $r^2 = 0.171$, $F = 16.892$, $P < 0.0001$; largest adults in 500-m intervals: $y = 10.335 + 0.002x$, $df = 16$, $r^2 = 0.344$, $F = 7.859$, $P = 0.0134$.

(Van Voorhies 1996), are unlikely to be implicated because all of these populations (Figs. 1, 2) live in very cold, nearly isothermal regions below the permanent thermocline (Sanders 1968). We suggest that the increase in adult size with depth may be caused by the steep gradient in nutrient input selectively favoring larger size for its metabolic and competitive advantages (Peters 1983). The density of polychaete worms, the primary diet of turrids, decreases exponentially with depth (Thistle et al. 1985). Larger size may confer ad-

vantages in increased mobility to forage on scarcer prey and the ability to exploit a wider range of prey sizes (Levinton 1982, 1987). Larger larvae would have similar advantages. At the time of settling on the bottom, they would have lower vulnerability to predators, greater ability to withstand starvation, greater mobility to locate food, and access to a larger range of food items (Spight 1976). Thus, the increase in size with depth at all stages of life may be a direct consequence of selection favoring larger size as an adaptation to lower food availability. This may apply both within species and among closely related species as they replace one another with depth on large bathymetric scales (Figs. 1, 2). Gastropod species also show an increase in geographic range size with depth (Etter and Rex 1990), thus making their sparse populations less vulnerable to local extinction, particularly when larvae have high dispersal potential, as in the turrids analyzed here.

The size-depth trends observed in deep-sea snails cannot be explained as a simple extension of the reduction in average organism size across the deep-sea threshold, as assumed in the size-structure hypothesis and later attempts to test it. The upper boundary of the deep-sea ecosystem occurs at approximately 200 m where the descent of the sea floor steepens from the outer continental shelf to the upper continental slope. The shelf-slope transition is a narrow zone of rapid environmental change and species turnover (Rex 1981). Although deep-sea and shallow-marine systems are ecologically coupled through nutrient cycles (Rowe and Pariente 1992), they are otherwise very different environments where quite distinct faunas have evolved (Gage and Tyler 1991). The Turridae is by far the most species-rich family of gastropods at bathyal and abyssal depths (Bouchet and Warén 1980). It is interesting that in coastal snail faunas, turrids are proportionately much less well represented and also quite small (Shimek 1983a,b,c). A similar, but even more striking, congruency of body size and taxonomic makeup occurs in bivalved mollusks. Both lamellibranch and protobranch bivalves inhabit inshore areas, but the much smaller protobranchs dominate almost completely in the deep sea (Allen and Sanders 1996). Taxonomic differences between coastal and deep-sea molluscan faunas may have a variety of underlying causes such as substrate preference and the ecological potential for different feeding types and reproductive modes. However, for gastropod and bivalved mollusks, which collectively represent a very broad range of lifestyles (Rex 1976), small body size appears to be a common shared characteristic associated with successful colonization of the deep sea. This raises the possibility that the diminutive size of most deep-sea organisms and size-depth clines within the deep sea may be produced by independent mechanisms that operate on different scales of time and space. Diminished average size at the deep-sea threshold may be the historical consequence of a biogeographic filter that selectively favors invasion of the deep sea by taxa composed of inherently small individuals. The more gradual clinal changes found in deep-sea gastropods may represent geographic population differentiation within species as a response to recent selection and the large-scale habitat partitioning among species that attends adaptive radiation along a depth gradient.

The adaptive significance of body size is a problem of

fundamental and growing interest in evolutionary ecology (Brown 1995; Rosenzweig 1995; Siemann et al. 1996; West et al. 1997). Recent insights have come almost exclusively from analyses of data on the terrestrial biota (Blackburn and Gaston 1994). Much less is known for marine systems. It is important not to generalize from one taxon to others. However, the remarkably consistent and unexpected size-depth trends that are revealed in gastropods by using precise standardized measurements of size should encourage similar studies on other groups of deep-sea invertebrates. For mollusks, the results presented here and by Rex and Etter (1998) suggest that coastal and deep-sea environments may be separate theaters of evolution where factors mediating colonization account for the major difference in body size. To the extent that evolution has unfolded independently in these two marine systems, it seems reasonable to expect a variety of bathymetric patterns of size to emerge in different deep-sea taxa depending on phylogenetic constraints, basic natural history, and physiology.

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